Flowers and insects. XIII.[1]

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DODECATHEON MEADIA L.—American cowslip, shooting-star. In his arrangement of floral mechanisms Delpino (2) recognizes a class of pendulous nodding or horizontal flowers upon which the visitors cling (apparrecchi prensili), which he divides into the borrage and the verbascum types (tipo borragineo, tipo verbascino). The former includes such flowers as *Dodecatheon*, *Cyclamen*, and *Solanum*, which the bees clasp in such a way as to receive the pollen upon the undersides of their bodies, and the latter contains flowers like *Verbascum* and *Tradescantia*, which are provided with hairs which afford a foot-hold.

Kerner (1) regards the reflexed petals as facilitating access to nectar and pollen, and this is true as regards the legitimate visitors. Intruders are much more effectually excluded than would be the case if the petals were less strongly reflexed, as in the flowers of *Erythronium.*[2] The approximation of the anthers in a compact cone also gives the flower a signal advantage over such a flower as *Ribes gracile*,[3] whose stamens being of the ordinary form permit the visits of a number of insects which the flower cannot utilize. The reflexed petals also render the nodding flowers much more conspicuous and attractive than they would be if the expanded petals faced the ground.

Loew (3) has figured and thoroughly described *Dodecatheon integrifolium* Michx. (=*D. Meadia* L.), *D. Jeffreyi* Moore (=*D. Meadia* var. *lancifolium* Gray), and an unnamed species from material growing in the Berlin Garden. To this I shall add an account of *D. Meadia* as observed under natural conditions in Illinois.. The plant is common in prairies and open woods, where it grows in rather large patches. The scapes rise from 3 to 6^{dm} and bear numerous, handsome flowers, which are white or rose color. The corolla has a short tube, which for

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[1]Contributions to an account of the ecological relations of the entomophilous flora and the anthophilous insect fauna of the neighborhood of Carlinville, Illinois.

[2]Bot. Gaz. 17:69. 1892.

[3]Ibid., 270.

about 3^{mm} is united with a tube formed by the monadelphous filaments. After separating from the stamen tube it is bent upon itself, and its lobes are strongly reflexed. At the flexure it is strongly thickened and marked with dark reddish purple. This portion of the corolla forms a foot-hold for the bees to cling to while sucking. The tube formed by the united filaments is about 5^{mm} long. The anthers are very rigid and are so closely approximated that they form a cone from 8 to 10^{mm} long. Exteriorly the stamen-tube is yellow, but the base of each anther is swollen and marked with dark purple. This part also serves as a foot-hold and as a path-finder. The stamen-tube with its cone of rigid anthers serves to conceal the nectar and to render it quite deep seated, for to reach the sweets the bees must force their proboscides between the anther tips.

The flowers are homogamous. Cross-pollination is secured by the stigma being 2 or 3^{mm} in advance of the anthers and having its surface directed away from them. According to Loew (3) spontaneous self-pollination may occur when the corolla falls.

During the blooming season, April 24 to May 24, the plant is in competition more or less severe with the following flowers, which are also adapted to bumblebees, no mention being made of those whose seasons overlap for only a short time with the first or last part of the season of *Dodecatheon:*

Delphinium tricorne, Geranium maculatum, Aesculus glabra, Astragalus Mexicanus, Baptisia leucophaea, Pyrus coronaria, Rubus villosus, R. Canadensis, Triosteum perfoliatum, Hydrophyllum Virginicum, Mertensia Virginica, Pentstemon pubescens, Monarda Bradburiana, Orchis spectabilis, Uvularia grandiflora and the introduced Trifolium pratense, Robinia Pseudacacia and Nepeta Glechoma.

The phaenological position of *Dodecatheon* exposes its flowers to bumblebee females, the workers only beginning to appear as the blooming time expires. It coincides pretty nearly with the flight of *Anthophora ursina*, and later overlaps with the early part of the flight of *A. abrupta*. *Synhalonia speciosa* and *S. belfragei* and *Osmia bucephala* fly throughout the period. These are the only long-tongued bees which could be expected to visit the flowers in my neighborhood. May 2, 5 and 8 I saw the flowers visited by the following:

Hymenoptera—*Apidæ:* (1) Bombus americanorum F. ♀, s., ab.; (2) Anthophora ursina Cr. ♀, s. and c. p.; (3) Synhalonia speciosa Cr. ♂, s., *Andrenidæ:* (4) Augochlora pura Say ♀, c. p., one.

Lepidoptera—*Rhopalocera:* (5) Colias philodice Gdt., s.

On the literature of *Dodecatheon* see:—

(1) Kerner, Die Schutzmittel des Pollens gegen die Nachtheile vorzeitiger Dislocation und gegen die Nachtheile vorzeitiger Befruchtung 38. 1873. Sep. a. d. Berichten des naturw. med. Vereines zu Innsbruck 2 and 3:—.1872.—(2) Delpino, Ulteriori osservazioni sulla dicogamia nel regno vegetale Pt. 2. fasc. 2: 295. 1875. Estratto dagli Atti della Soc. Ital. delle Sci. Nat. in Milano 16 and 17:—.1873–1874.—(3) Loew, Blüthenbiologische Beiträge I, 17–21. Sep. aus Pringsheim's Jahrbucher 22:—.1891. (Abstract in Just's Bot. Jahresbericht 19[1]: 416.)

STEIRONEMA CILIATUM Raf.—The observations which have been recorded seem to show that the adaptation for cross-pollination in *Lysimachia* and *Steironema* consists in the stigma being so far advanced above the anthers that self-pollination never or rarely occurs, as in Müller's large form of *L. vulgaris* (3, 16), or from proterogyny, as in *L. thyrsiflora* (Warming 10 and MacLeod 24) and in our *S. lanceolatum, longifolium* (23) and *ciliatum.* A less conspicuous form of *L. vulgaris*, which grows in situations unfavorable for insect visits is regularly self-fertile. Other species are homogamous and self-pollinating, as *L. nummularia* (Warming 10) and *nemorum* (Kerner 22).

According to Bonnier (11) in *L. vulgaris* nectar is secreted by the ovary and escapes through stomata in the epidermis, but in most cases it is wanting, or exists in quantity imperceptible by ordinary means, though the visits of male bees seem to indicate its presence (3, 16, 23). The part played by the papillæ in the attraction of insects (Kerner 22) is even more doubtful. I have seen no evidence of this in our species. The pollen is by far the most important, for by attracting the females of *Macropis* it has given rise to an interesting case of mutual economic correlation. Our species of *Steironema* (23) and the European *L. vulgaris* (3, 16, 24, 27) and *punctata* (4) are visited almost exclusively by bees of this

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[4]As a substitute for a more extended review it is proposed to give an index to the literature of each genus, arranged chronologically, and it is hoped that the index will contain at least the principal references. Use has been made of the Bibliography compiled by D'Arcy W. Thompson, published in the translation of Müller's Befruchtung der Blumen, and giving the titles of books, etc. published up to 1883; of MacLeod's continuation of Thompson's list for the period 1833-1889, Bot. Jaarboek, 1890; of the abstracts by Müller and Dalla Torre in Just's Bot. Jahresbericht and those of Ludwig and others in the Bot. Centralblatt. I am under obligations to Prof. Wm. Trelease for access to the literature contained in the library of the Missouri Botanical Garden.

Abstracts are not cited unless they contain information on the genus being indexed. Information about contents of papers, etc., when given in the text, is not repeated in the index.

genus. I have mentioned (23) the flowers on which species of *Macropis* have been observed. Patton (12) states that Dufour found both sexes of *M. labiata* on flowers of *Alisma plantago*, and Schenk one or both on *Bryonia*, *Rubus caesius*, *Cirsium arvense* and *Picris*, but no one has seen a female *Macropis* collecting pollen of any flower except *Lysimachia* and *Steironema*.

Steironema ciliatum agrees in all essential particulars with *S. lanceolatum* (23). It grows taller and has larger flowers. In Connecticut Patton (13) saw the flowers visited by *Macropis ciliata* Pttn. ♀ and by *M. patellata* Pttn. ♂. In Illinois I have seen them visited by *M. steironematis* Rob. ♂♀, the female collecting pollen. The latter bee does not seem to have a decided preference for yellow, for all of the other flowers I have taken it on are white (23).

On the literature of *Lysimachia and Steironema* see:—

(1) Sprengel, Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen. 1793. *L. quadrifolia* and *vulgaris*, 104.—(2) Kerner, Die Schutzmittel des Pollens 27. 1873.—(3) Müller, Befruchtung der Blumen durch Insekten. 1873. *L. vulgaris* and *nummularia*, 348–9.—(4) Delpino, Ulteriori osservazioni nel sulla dicogamia regno vegetale Pt. 2. fasc: 1: 212, 321. Estr. dagli Atti della Soc. Ital. d. Sci. Nat. 17:—.1874. Visits of *Macropis* to *L. vulgaris* and *punctata* observed by Piccioli, Müller and Delpino in Westfalia, at Firenze and Vallombrosa.—(5) Lubbock, British wild flowers considered in relation to insects. 1875. *L. vulgaris*, visits of *Macropis*, 21; Müller's two forms, 126.—(6) Darwin, The variation of animals and plants under domestication 2: 154. 1876. 2d edit. *L. nummularia*, sterility.—(7) Darwin, The different forms of flowers on plants of the same species. 1877. *L. vulgaris*, Müller's two forms, 4, 342.—(8) Müller, Das Variiren der Grösse gefärbter Blüthenhüllen und sein Einfluss auf die Naturzüchtung der Blumen. Kosmos 2: 11–25, 128–139. 1877. *L. vulgaris*. (Abstract in Just's Bot. Jahresbericht 5¹: 740.)—(9) Henslow, On the self-fertilization of plants. Trans. Linn. Soc. II. Bot. 1: 328, 377. *L. vulgaris*, Müller's two forms. 1877.—(10) Warming, Smaa biologiske og morfologiske bidrag. Bot. Tidsskrift III. 2: 108–130. 1877. (Just's Bot. Jahresbericht 5¹: 745–6.)—(11) Bonnier, Les Nectaires. Extrait des Ann. des Sci. Nat. Bot. VI. 8: 140. 1879. (Just's Bot. Jahresbericht 7¹: 120.)—(12) Patton, Observations on the genus Macropis. Am. Journ. Sci. and Arts. III. 18: 211–14. 1879. *L. vulgaris* and *S. ciliatum*. (Just's Bot. Jahresbericht 7¹: 145.)—(13) Patton, Description of the species of Macropis. Ent. Monthly Magazine 17: 32–33. 1880.—(14) Dufour, Existence de tensions chez certaines fleurs. Etude d' anatomie et de physiologie végétales, desertation inaugurale, 42–46. 1882. (Just's Bot. Jahresbericht 9¹: 500.)—(15) Müller, Weitere Beobachtungen über Befruchtung der Blumen durch-Insecten 3: 65. 1882. Scp. aus dem Verh. des naturhist. Ver. der. preuss. Rheinl. u. Westf. *L. vulgaris*, visitors.—(16) Müller, The fertilization of flowers

389–390. 1883. *L. vulgaris*, pollination, *L. nummularia* and *thyrsiflora*, ref. (6) and (10).—(17) MacLeod, Untersuchungen über die Befruchtung einiger phanerogamen Pflanzen der Belgischen Flora. Bot. Centralblatt **23**: 366. 1885. *L. vulgaris*, autogamy. (Just's Bot. Jahresbericht 13^1: 740.)—(18) MacLeod, Nouvelles recherches sur la fertilisation de quelques plantes phanérogames. Arch. de Biol. **7**: 156. 1886. *L. vulgaris*.—(19) Kirchner, Neue Beobachtungen über die Bestäubungseinrichtungen einheimischer Pflanzen. Progr. des 68 Jahresfeier der kgl. Württemb. landwirtsch. Akademie Hohenheim. 1886. *L. nemorum*, no nectar. (Just's Bot. Jahresbericht 14^1: 791.)—(20) Jordan, Die Stellung der Honigbehälter und die Befruchtungswerkzeuge in den Blumen 51. Sep. aus Flora 69: 1886. *L. punctata*, nectar receptacles of doubtful occurrence.—(21) Halsted, Observations upon pollen measurements. Bull. Torr. Bot. Club **16**: 135. 1889. *S. lanceolatum*, (Just's Bot. Jahresbericht 17^1: 523.)—(22) Kerner, Pflanzenleben. **2**:—. 1891. (Just's Bot. Jahresbericht 17^1: 528. **18**: 484.) *L. ciliata* Protection of pollen by nodding of fls., 118. *L. thyrsiflora*, *ciliata*, attraction by papillæ, 166. *L. nemorum*, spontaneous self-pollination, 338. *L. nummularia*, 398.—(23) Robertson, Flowers and insects. X. Bot. Gaz. 18 47–48. 1893. *S. lanceolatum*, *longifolium*, *ciliatum*, *L. quadrifolia*, *vulgaris*, *nemorum*, *nummularia*. (Bot. Centralblatt **55**: 101.)—(24) MacLeod, Over de bevruchting der bloemen in het Kempisch gedeelte van Vlaanderen. Bot. Jaarboek **5**: 443–444. 1893. *L. vulgaris*, *nemorum*, *nummularia*, *thyrsiflora*. (Bot. Centralblatt **56**: 177.)—(25) Knuth, Blumen und Insekten auf den Nordfriesischen Inseln 120. 1894. *L. vulgaris*, autogamous form on Sylt.—(26) Loew, Blütenbiologische Floristik des mittleren und nördlichen Europa sowie Grönlands. 1894. *L. vulgaris*, 161. *L. nummularia*, *nemorum*, *thyrsiflora*, *ciliata*, 319.—(27) Knuth, Weitere Beobactungen über Blumen und Insecten auf den Nordfriesischen Inseln. Schr. d. Nat. V. f. Schleswig-Holstein **10**: 229, 239. 1895? Correlated presence or absence of *Macropis* and *Lysimachia* on certain islands, etc.

ENSLENIA ALBIDA Nutt.—The plants are common on creek-banks, often climbing high, and blooming from July 12th to August 22. The flowers are white and are arranged in small umbel-like clusters. The petals are erect, and their tips are bent aside, out of the way of the passage leading to the nectar. The divisions of the crown are petal-like and erect, the central portion being produced above into two long appendages. On each side there is a wing-like portion which is grooved on the inner face, where the nectar is secreted and lodged. Each wing-like part, with the one of the next division forms a more or less well defined passage, which guides the bee's proboscis to the nectar. This is situated so near the angles of the wings of the approximated anthers that, when the proboscis is withdrawn, some slender appendage is quite likely to be caught between the divergent angles of the anther wings and guided by them into the cleft of the little black corpusculum which lies at the top of the slit. The gynostegium is quite slender and is tipped by five white

appendages. These, with the ten flexuous tips of the crown divisions and the five erect petals, give the flower a soft, white appearance and conceal the complicated mechanism within, while they also render a little more evident the passage which leads to the nectar.

When a corpusculum with its pair of pollinia is withdrawn, it shows an unusually short retinaculum, which from its attachment to the corpusculum curves outward and a little downward and is inserted a little below the apex of the pollinium. The apex of the pollinium thus forms a very conspicuous knee, which stands at right angles to the axis of the corpusculum, and this knee is the part which is caught by the anther wings and thus causes the insertion of the pollinium. I find no evidence whatever that the original appendage to which the corpusculum becomes attached ever again enters the slit, or that the pollinia are introduced in pairs. When the pollinia are thoroughly dried, their planes are commonly perpendicular to each other, or they sometimes lie in nearly the same plane. The knees, therefore, project in different directions, and this increases the chances of one of the pollinia being inserted into the stigmatic chamber. There is nothing to render it probable that the bee's proboscis will be introduced in the same relative position, and so there is no advantage in both of the knees, or either of them, turning to the same side. In *Asclepias* and *Acerates*, in which the corpuscula are usually attached to short hairs on the legs, or other parts of the body, as in *Acerates longifolia*,[5] it is important that the knees should turn away from the part to which they are attached, for this is the only side on which they are likely to be caught by the anther wings. In large flowers, like *Asclepias Sullivantii*, in which the corpuscula are attached to the bee's claws, the bees commonly clasp the flowers so that the legs are guided upwards between the hoods. The movement of the knees which brings them near together results in turning them inwards, in which position they are more likely to be brought to the stigma. In *Enslenia* the corpuscula are attached so near to the end of the proboscis that there does not seem to be any advantage in turning in any particular direction, though they are slightly turned towards the side on which the corpusculum is attached.

Müller and Corry erroneously supposed that the movement

[5] Bot. Gaz. **12**: 245. 1887.

of the pollinia of *Asclepias*, which approximates them, is intended to facilitate the introduction of both pollinia into the same stigmatic chamber. In *Cynanchum vincetoxicum*,[6] whose mechanism in a general way resembles that of *Enslenia*, Müller states that the retinacula bend so that the pollinia come close together. The flowers are adapted to carrion flies, Muscidæ, Sarcophagidæ, etc., and I suspect that the movement is merely to turn the knees away from the proboscis. Müller's account of the pollination of *Cynanchum* seems to me to be just as erroneous as that of *Asclepias Cornuti*. In the normal pollination of any asclepiad I doubt if it can be shown either that the part to which the corpusculum is attached is again caught by the wings, that the corpusculum ever enters the slit, or that both pollinia together are ever introduced into the same stigmatic chamber.

The flowers of *Enslenia* are visited principally by bees of the genus *Halictus*. These insects readily remove the corpuscula, which are found attached to the palpi, the tips of the laminæ, or other fine divisions of the proboscis. *Myzine sexcincta* was abundant on the flowers, but I could find no examples bearing corpuscula. The following list was taken on July 14th, 20th, and August 22d; the insects bearing corpuscula are indicated by !

Hymenoptera—*Andrenidæ:* (1) Prosopis pygmaea Cr. ♂; (2) P. modestus Say ♀, !; (3) Halictus confusus Sm. ♂♀, ab., !; (4) H. zephyrus Sm. ♂♀, ab., !; (5) H. stultus Cr. ♂♀, ab., !; (6) H. tegularis Rob. ♂♀, !; (7) H. cephalicus Rob. ♀; (8) H. platyparius Rob. ♀; (9) Augochlora viridula Sm. ♂♀; *Eumenidæ:* (10) Odynerus sp.; *Scoliidæ:* (11) Myzine sexcincta F., ab.

Diptera—*Empidæ:* (12) Empis clausa Rob. MS; *Bombylidæ:* (13) Anthrax fulvohirta Wd., !

Carlinville, Ills.

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[6] Müller, Alpenblumen, 350. Fertilization of Flowers, 401.